

Body size, body size ratio, and prey type influence the functional response of damselfly nymphs

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Abstract Predator–prey interactions play a crucial role in structuring food webs, and the functional response is one way to measure the strength of this interaction. Here, we examine how predator and prey body size affects the functional response of a generalist predator—damselfly nymphs—feeding on three prey types: copepods, *Daphnia*, and *Chydorus*. Our results suggest that consumption of copepods is independent of predator body size, while increased predator body size is associated with an increased space clearance rate for *Daphnia* and a reduced space clearance rate for *Chydorus*. When considered together, foraging rates on *Daphnia* and *Chydorus* (both cladocerans) are consistent with a hump-shaped functional response, with peak foraging rates occurring at an intermediate predator–prey size ratio. Thus, although most food web theory assumes allometric

predator–prey links or peaked functional responses at intermediate predator–prey size ratios, our results suggest that both relationships may occur in food webs, in addition to size-independent functional responses.

Keywords *Daphnia* · *Chydorus* · Copepods · Handling time · Predator–prey interaction

Introduction

Predator–prey interactions play critical roles in ecological communities, forming the links within food webs (Levi and Wilmers 2012), driving population dynamics (Jost et al. 2005), and shaping landscapes (Ripple and Beschta 2004). The strength of those interactions—or interaction strength—is some measure of how important a particular predator–prey interaction is to the flow of energy through that part of the food web (Novak and Wootton 2010; Gilbert et al. 2014). Interaction strengths, therefore, play a role in setting food web properties and dynamics (McCann et al. 1998; Gilbert et al. 2014). Moreover, predator and prey traits—such as offensive or defensive structures and body size—play a strong role in setting interaction strengths (Kopp and Tollrian 2003; Ham-mill et al. 2010; Rall et al. 2011; Kalinoski and DeLong 2016).

The functional response—the relationship between prey density and predation rate—is one tool for measuring the strength of interactions between predator and prey (Holling 1959). A Type I functional response is a linear relationship between prey density and predation. A Type II functional response is asymptotic, saturating once time (not prey availability) becomes the limiting factor. The Holling disc equation describes the Type II functional response,

$$f_{pc} = \frac{aR}{1 + ahR}, \quad (1)$$

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Food webs are structured by foraging interactions that depend on a variety of predator and prey traits. Body size is a key trait that influences who eats whom, and by how much, in most food webs. Our research reveals unexpected diversity in the way predator and prey body size influence foraging links in food webs, contradicting assumptions of universal allometric or unimodal responses to predator and prey body size. We propose a new mechanistic functional response model that can elucidate how variation in foraging behavior can generate diverse body size effects on functional responses.

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where f_{pc} is per capita foraging rate, a is the space clearance rate, R is resource (prey) density, and h is handling time. The space clearance rate is how much space a predator clears of prey per unit time, and the handling time is the predator's time investment per prey consumed.

A variety of traits influence the shape of functional responses. Body masses of predator and prey influence both space clearance rate and handling time, usually as a power law function of predator body size (Thompson 1975; DeLong and Vasseur 2012; Rall et al. 2012; DeLong 2014). Typically, handling time decreases as predator size increases or prey size decreases. This is intuitive: smaller predators may struggle to restrain prey, and larger prey often can overwhelm potential captors. Similarly, larger predators may encounter prey at greater rates or detect them from farther away (McGill and Mittelbach 2006), allowing space clearance rate to increase with body size. Alternatively, the ratio of predator to prey body size may generate a peak in space clearance rate at an intermediate, optimum size (Spitze 1985; Tripet and Perrin 1994; Persson et al. 1998; Wahlström et al. 2000; Vucic-Pestic et al. 2010; Barrios-O'Neill et al. 2016).

Prey characteristics other than body size (including prey defenses and identity, predator age, and body temperature) also may affect functional responses (Hammill et al. 2010; Rall et al. 2011; Kalinoski and DeLong 2016). Because of these trait effects, and because most previous size-related functional response experiments focus on a single predator–prey combination even though predators in a natural setting encounter a variety of prey species of varying sizes, here we examined how predator size and predator–prey size ratio affects functional response parameters across prey types. We studied damselfly nymphs (family *Coenagrionidae*, mostly *Ischnura verticalis* and *Enallagma civile*) feeding on three types of crustacean prey: *Daphnia* sp., *Chydorus* sp., and copepods. *Daphnia* and *Chydorus* are both cladocerans and are more closely related to each other than either is to copepods. These three prey types were chosen because they often co-occur in freshwater ponds and represent common prey for damselfly nymphs. Because they vary in body size, these prey types also allow comparison of body size effects both within and across taxonomic groups. Specifically, we tested for effects of body size on functional response parameters for all three prey types. Our results suggest variable body size effects, so we also propose a mechanistic model for understanding a hump-shaped response of the functional response parameter a (space clearance rate) and apply it to our data on cladocerans.

Materials and methods

Damselfly nymphs (avg. length 1.23 ± 0.26 cm) were collected from ponds 1.5 km east of Lake Ogallala, Nebraska

and housed indoors individually in 120-mL plastic cups. Damselfly nymphs used in this study varied in species, age, and other factors but were assigned randomly to treatments such that predator identity would increase variance but not bias our results. Cups were filled with 60 mL of pond water and contained one 5–8-cm dried grass stalk to serve as a resting perch. Loose lids allowed ventilation. *Daphnia* (average width: 0.49 mm), *Chydorus* (0.25 mm), and copepods (0.19 mm) collected from Lake Ogallala and ponds north of the Lake McConaughy visitors' center were maintained in similar plastic cups. Predators and prey were kept indoors at approximately 23 °C with a photoperiod consistent with natural daylight hours (approx. 15:9 h L:D) for the duration of the experiment (14–16 June 2016). Experimental arenas consisted of Petri dishes filled to a depth of 0.5 cm with filtered pond water. Nymphs were starved for 18 h in filtered pond water before foraging trials.

To account for possible spatial constraints on foraging behaviors, we used three arena sizes (6, 10, and 16 cm diameter) for foraging trials and tested for effects of arena size on functional response parameters. We chose initial prey numbers to create similar density ranges (~ 0.01 – 0.4 prey/mL) across dish sizes, using between one and five prey individuals of the same type in foraging trials with the small dishes, 1–15 prey in medium dishes, and 1–35 prey in large dishes. We first added the prey and then transferred one nymph to each arena, covered the dish, and left the predator undisturbed. After 3 h, we carefully removed the nymph and counted the remaining prey. For each prey type, we observed one predator-free medium dish with ten prey individuals after 3 h to ensure that background mortality was negligible and that live prey could be recovered and counted accurately. Although we tested some nymphs in more than one trial, no nymphs experienced a prey type or arena size more than once. For the copepods, *Daphnia*, and *Chydorus*, respectively, we recorded data from 26, 38, and 28 trials in large dishes, 32, 35, and 26 trials in medium dishes, and 26, 37, and 25 trials in small dishes. A limited number of damselflies died or emerged as adults before completion of the experiment, and data points associated with these damselflies were discarded.

We photographed each predator prior to the start of the experiment and subsequently measured head width (taken as the widest part of the head, from the outside of one eye to the outside of the other) using ImageJ (Rasband 2017). Head width was chosen as a representative measure of body size because it presumably reflects the size of prey that the predator can consume (Thompson 1975). Representatives of each prey type were also photographed and the widest part of the body measured. Body size ratio was calculated for each predator as predator head width over average prey body width. Due to the large number of prey used per experiment, we were unable to quantify the width of each prey item.

We used non-linear least squares fitting in Matlab to fit the data on prey abundance to foraging rates separately for all prey types and dish sizes. During the experiments, however, we did not replenish prey as they were eaten by nymphs. Therefore, we fit our data to the lambert W modification of Roger’s predator equation (Rogers 1972; Bolker 2011) (Eq. 2), which accounts for prey depletion, instead of the standard Type II functional response (Eq. 1):

$$N_e = N_0 - \frac{W(ahN_0e^{-a(t-hN_0)})}{ah}, \tag{2}$$

where N_e is the number eaten, N_0 is the initial number of prey provided, and t is the duration of the foraging experiment.

Estimates of space clearance rate increased with arena size, possibly because nymphs or prey exhibit more natural movement behaviors as the experimental arena approaches natural space constraints (i.e., the size of a pond), presumably capping once the arena is large enough that the nymphs are no longer inhibited by the arena’s edges. In addition, these fits suggested that the use of small arenas generated very low precision parameter estimates with possible biases generated by the complete depletion of prey. To obtain a more accurate estimate of functional response parameters, data points from the large and medium dishes were pooled using the following method. The parameters from the large dishes were used to generate expected large-dish foraging rates for the densities to which the medium dish damselflies were exposed. Residuals were used to scale the resultant medium-dish data points up or down, accordingly. Due to their variability, data points obtained from small dishes were not used for further analysis. Medium and large dish data were then combined.

To determine the effect of body size, we then fit the combined data to models that incorporate size dependence of handling time (h ; Eq. 3) and space clearance rate (a ; Eq. 4) into the Roger’s predator equation using power law functions of predator head width. That is, we substitute h_0M^Y for h and a_0M^Y for a :

$$N_e = N_0 - \frac{W(ah_0M^Y N_0e^{-a(t-h_0M^Y N_0)})}{ah_0M^Y} \tag{3}$$

$$N_e = N_0 - \frac{W(a_0M^Y hN_0e^{-a_0M^Y (t-hN_0)})}{a_0M^Y h} \tag{4}$$

However, space clearance rate can peak when predators are intermediate in size relative to their prey, generating a hump-shaped relationship between space clearance rate and predator–prey size ratio (Spitze 1985; Wahlström et al. 2000; Vucic-Pestic et al. 2010). To determine if this was the case in our data, we fit both a linear polynomial and a polynomial with a quadratic term to the pooled cladoceran data.

This quadratic polynomial and other current models used to describe a hump-shaped functional response describe the shape of the response rather than the underlying foraging processes (Persson et al. 1998; Wahlström et al. 2000; Vucic-Pestic et al. 2010; Barrios-O’Neill et al. 2016). A mechanistic model of the dependence of space clearance rate on predator–prey size ratios could shed some light on how body size ratios influence functional responses and direct additional experiments. As an alternative, then, we suggest that the hump shape could arise from the mechanics of foraging described by a common equation for space clearance rate. Space clearance rate can be given by

$$a = p_s p_a d \sqrt{v_r^2 + v_c^2}, \tag{5}$$

where d is the maximum distance at which the predator can detect the prey, p_a is the probability of attack given detection, p_s is the probability of successful capture given attack, v_c is the velocity of the consumer (predator) and v_r is the velocity of the resource (prey) (Aljetlawi et al. 2004; Pawar et al. 2012). It is widely expected that body size has effects on the physical aspects of foraging represented in the model such as searching speeds (v_c), detection distances (d), and the ability to subdue prey (p_s) (McGill and Mittelbach 2006; Dell et al. 2014; DeLong 2014).

In Eq. 5, the combination of p_a and p_s is the probability of a successful attack. This is not likely to be a simple allometric function of predator size. Rather, the choice to attack likely reflects some combination of energetic return, prey defenses, likelihood of success, and opportunity costs if other prey are available (Charnov 1976), while the probability of success may depend on predator or prey size and the presence of defensive traits in the prey. We suggest that this could be modeled as $\frac{1}{1+e^{c_1 M_r}}$, where c_1 is a constant that sets the slope of the transition from 1 to 0 such that at a low size ratio the probability of a successful attack is 1 and at a higher size ratio it transitions to 0. Depending on the value of c_1 , the effect of body size ratio on the probability of successful attack on increasingly small prey could be positive, negative, or neutral depending on the costs and benefits of choosing relatively small prey.

The combination of $d \sqrt{v_r^2 + v_c^2}$ describes the space in which prey are detected, which should increase with predator size as larger predators move more quickly and can detect prey across longer distances. Thus, we suggest that this part of the equation could be modeled as a standard power law function of body size ratio, $c_2 M_r^Y$, where M_r is the body size ratio, c_2 is a constant, and Y is a scaling exponent. Together, these two functions can provide a description of how the space clearance rate could be a hump-shaped function of body size ratio:

$$a(M_r) = \frac{1}{1 + e^{c_1 M_r}} c_2 M_r^Y. \tag{6}$$

Fig. 1 Functional responses for copepods, *Daphnia*, and *Chydorus* for small (6 mm), medium (10 mm), and large (16 mm) Petri dishes. Fits to the data are for the Roger's predator equation (Eq. 4)

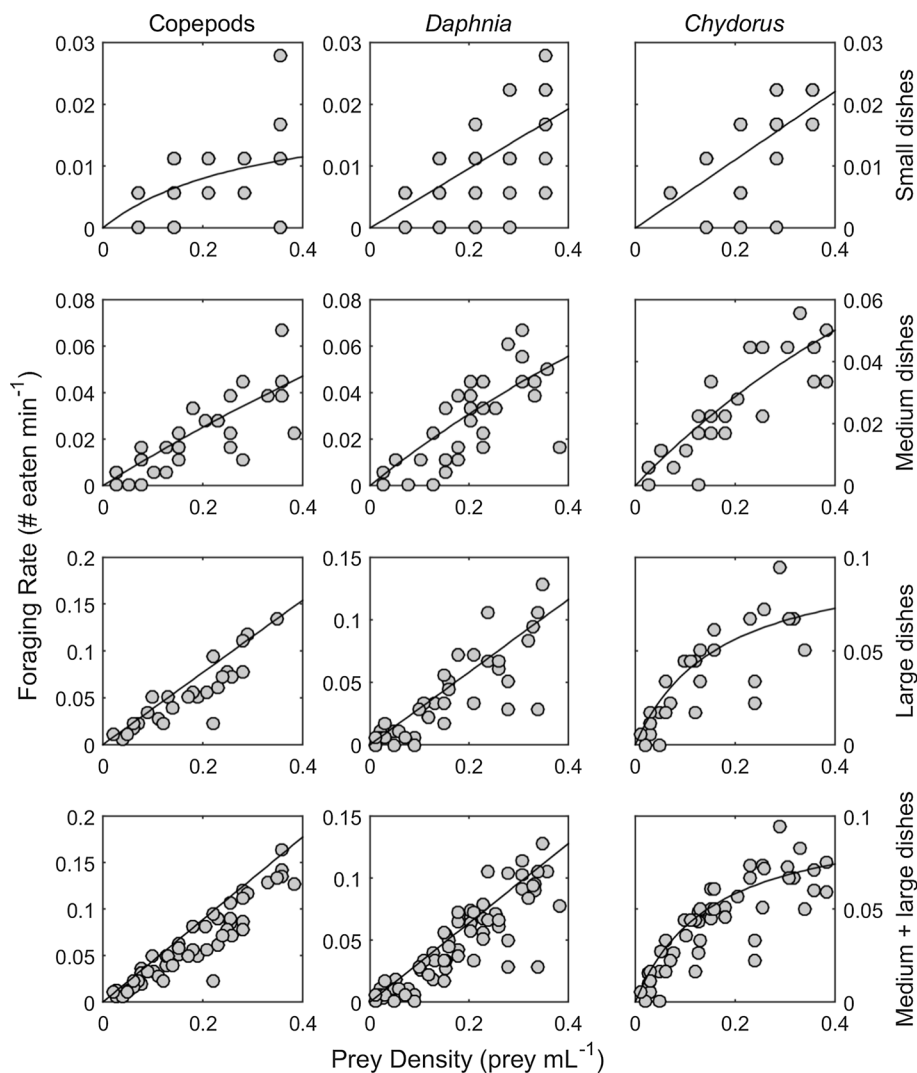
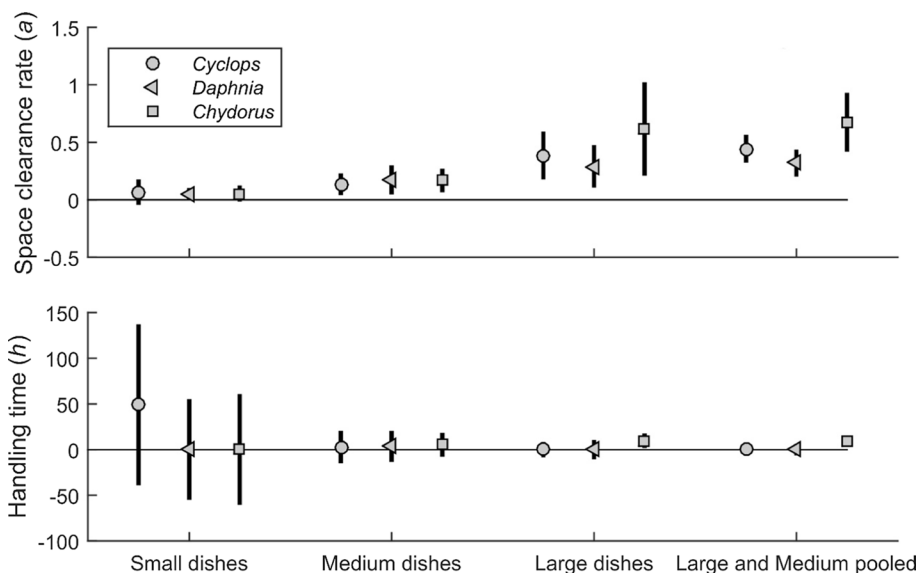


Table 1 Fits of functional response models (equation # refers to equation in the text) by prey type

Equation	Size dependence	a/a_0 (95% CI)	h/h_0 (95% CI)	Υ (95% CI)	R^2	AICc	$\Delta AICc$
Copepods							
2	None	0.44 (0.34, 0.55)	0.00 (-2.31, 2.31)		0.88	-476.5	11.7
3	Handling time	0.44 (0.39, 0.50)	41.69 (-9.0 × 10⁴, 9.0 × 10⁴)	7.02 (-1.91 × 10³, 1.93 × 10³)	0.88	-487.5	0.7
4	Space clearance rate	0.36 (0.18, 0.55)	1.4 × 10⁻⁷ (-2.3, 2.3)	-0.13 (-0.46, 0.19)	0.89	-488.2	0
Daphnia							
2	None	0.32 (0.22, 0.42)	0.00 (-4.08, 4.08)		0.76	592.28	4.1
3	Handling time	0.32 (0.29, 0.35)	0.05 (-2.0 × 10 ⁶ , 2.0 × 10 ⁶)	13.5 (-2.4 × 10 ⁷ , 2.4 × 10 ⁷)	0.76	-590.0	6.4
4	Space clearance rate	0.65 (0.19, 1.12)	9.4 × 10⁻⁷ (-3.9, 3.9)	0.52 (0.095, 0.94)	0.78	-596.4	0
Chydorus							
2	None	0.67 (0.44, 0.91)	9.74 (7.03, 12.45)		0.76	-476.5	16.4
3	Handling time	0.66 (0.48, 0.85)	55.04 (9.8, 100.24)	1.23 (0.61, 1.86)	0.83	-492.9	0
4	Space clearance rate	0.13 (0.02, 0.24)	8.59 (6.1, 11.1)	-1.04 (-1.61, -0.47)	0.81	-486.6	6.3

AIC values for small sample sizes indicate best supported models, in bold. There are no significant size effects for the copepod functional response, although models with these effects are better supported by AICc

Fig. 2 Mean and 95% confidence intervals for the functional response parameters (space clearance rate, top, and handling time, bottom) for copepods, *Daphnia*, and *Chydorus* for small (6 mm), medium (10 mm), and large (16 mm) Petri dishes. The far right section shows fits for the data from medium and large dishes rescaled and combined (see text)



We can then incorporate Eq. 6 into 2 to yield:

$$N_e = N_0 - \frac{W\left(\left(\frac{1}{1+e^{c_1 M_r}} c_2 M_r^Y\right) h N_0 e^{-\left(\frac{1}{1+e^{c_1 M_r}} c_2 M_r^Y\right)(t-hN_0)}\right)}{\left(\frac{1}{1+e^{c_1 M_r}} c_2 M_r^Y\right) h} \tag{7}$$

which we then fit to the pooled cladoceran data.

Results

Nymphs showed a Type I functional response for *Daphnia* and copepods (that is, handling time was not significantly different from 0) and a Type II functional response for *Chydorus* (Table 1 in the ESM, Figs. 1, 2). Nymph head width increased space clearance rate for *Daphnia* and decreased it for *Chydorus*, and was unrelated to space clearance rate for the copepods (Table 1, Fig. 3). In contrast, nymph head width increased handling time for *Chydorus* and had no effect on *Daphnia* and copepod handling times (Table 1).

AICc values show that fit with a quadratic term is better supported than a linear fit ($\Delta AICc = 15$), suggesting that when foraging on cladocerans, damselfly space clearance rates show a hump-shaped response to body size ratio. The mechanistic hump-shaped model, Eq. 7, provides a better-supported description of the functional response data than Eq. 4, where space clearance rate was just a power law function of body size ratio ($\Delta AICc = 10$) (Fig. 4). However, Eq. 7 was not different from Eq. 3, which had handling time as a power law function of body size ratio ($\Delta AICc = 1$).

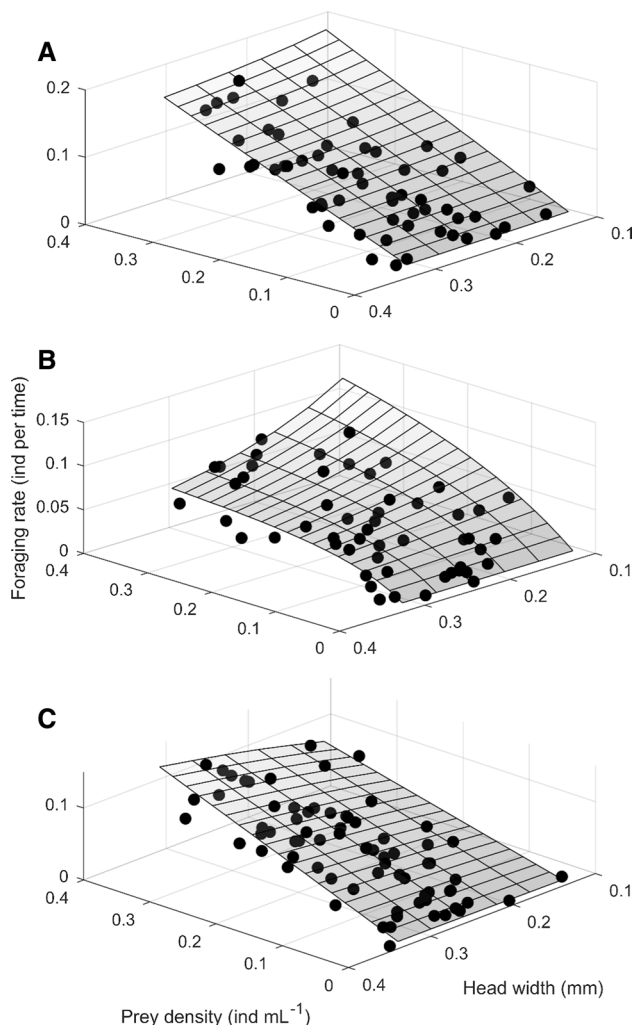


Fig. 3 a Functional response of copepods by body size ratio. b Functional response of *Daphnia* by body size ratio. c Functional response of *Chydorus* by body size ratio

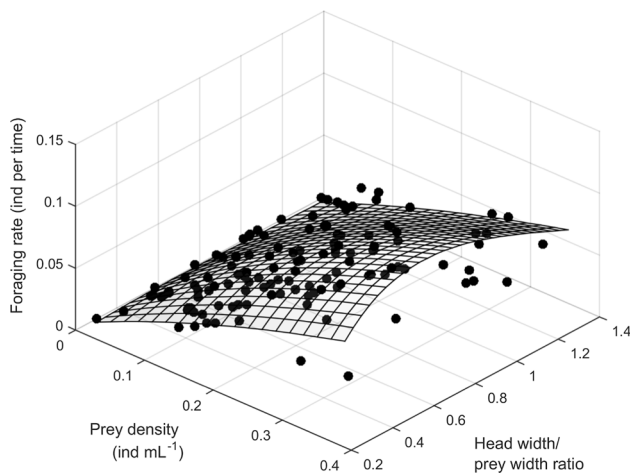


Fig. 4 Functional response of combined cladocerans (*Daphnia* and *Chydorus*) by body size ratio (predator head width/prey body width), fitted to the hump-shaped model (Eq. 7)

Discussion

We found variable body size dependence of functional response parameters for damselfly nymphs feeding on copepods, *Daphnia*, and *Chydorus*. Although body size is typically positively associated with space clearance rate across species, and for damselfly nymphs within species (Thompson 1975), within the three prey types tested we found positive, negative, and no effects depending on prey type (Fig. 3). These results both conflict with and are consistent with different views on the expected effect of body size on functional response parameters.

Our results supported the mechanistic hump-shaped model (Eq. 7) over Eq. 4, where space clearance rate was just a power law function of body size ratio. Thus, in our view the model suggests that increasing predator size may increase the frequency of successful attacks, but at increasingly larger size predators would attack less, reducing p_a and dropping the space clearance rate down despite the physical effects of larger size. Thus, although previous research has shown the importance of body size in determining foraging of aquatic insects (e.g., Thompson 1975; Spitze 1985), our results support both an allometric view of body size dependence and an intermediate peak for size ratios, depending on the taxonomic scale of observations and the type of prey considered (Vucic-Pestic et al. 2010; DeLong and Vasseur 2012). However, the insignificant $\Delta AICc$ between the mechanistic hump-shaped model and Eq. 3, where handling time is a power law function of body size ratio, suggests that we still need to do more to understand the combined, and possibly interacting, effects of predator and prey body size on functional responses. Further developing a mechanistic hump-shaped model that accurately describes functional

response data will require more detailed work focusing on the size-dependence of foraging components including attacks, success rates, movement rates, and detection. Such an approach would also facilitate a greater understanding of the dynamic consequences of hump-shaped body size effects on functional responses (Barrios-O'Neill et al. 2016).

Unlike the cladocerans, there was no effect of size on space clearance rate when damselflies consumed copepods. This size independence suggests that there are either no size effects in searching, detecting, and attacking copepods, or that there are multiple effects that cancel out. Copepods demonstrate a powerful escape response, yet they were captured regularly and nymphs showed a high space clearance rate when eating them. The copepods overall were relatively small, but copepods may be equally difficult to catch at any size, or hungry predators may attempt to catch cyclops of any size. Nonetheless, a hump-shaped response may become more apparent if a wider range of body size ratios (an increased number of larger cyclops and/or smaller damselflies) were sampled.

A hump-shaped function could also relate predator–prey size ratio to handling time. We did not focus on this here because (1) functions connecting predator or prey body size to the mechanisms of handling time have not been derived, and (2) our data on copepods and *Daphnia* did not allow us to calculate handling times for these two prey types. While it is possible that nymphs really did show a Type I functional response for these prey types, these functional responses are relatively uncommon and generally result when higher prey densities are needed to reveal a handling time limitation (Jeschke et al. 2004). Additionally, handling time may increase or decrease with predator size (DeLong and Vasseur 2012; DeLong et al. 2015), so we might expect a handling time limitation to become apparent in experiments with smaller or larger damselflies. Alternatively, foraging trials in larger arenas could potentially confirm the absence of handling time, as our experiment demonstrates that increasing arena size effectively tightens handling time confidence intervals (Fig. 1).

We focused on a set of predator and prey species that coexist widely in natural temperate ponds, and our results likely reflect real food web interactions. Our results suggest that traditional assumptions of either allometric or hump-shaped functional responses may often not reflect the diversity of size-dependent functional responses in real food webs. This result holds for damselfly nymphs as a group, even though trait and behavioral variation within and across species might influence foraging behaviors and the functional response (Jeffries 1990; Gibert and Brassil 2014; Start and Gilbert 2017). We suggest that one reason for this is the variability in body size dependence of the underlying components of predation (searching velocity, detection distance, and the choice to attack and the success of those

attacks). Understanding these underlying processes may be a useful way of making more accurate assumptions about the size dependence of foraging links in food webs (Cohen et al. 2003; Brose et al. 2006; Petchey et al. 2008; Allhoff et al. 2015).

Finally, our results call attention to the choice of arena size when estimating the functional response. Although simulations have found small effects of patch size on interaction strengths (Li et al. 2017), our results show that estimates of interaction strengths in the laboratory may depend strongly on the choice of arena size, therefore, supplementing these findings with additional experimentation is critical. We found that larger arenas produced less noisy and higher estimates of functional response parameters, possibly due to a smaller effect of arena sides on the behavior of the predator and prey in the larger dishes. Nonetheless, our results show that arena size is a seriously overlooked variable with profound effects on functional response parameter estimates. We suggest that larger arenas will generally be more reflective of natural conditions, but confirming this will likely require a series of experiments to determine how arena size mechanistically affects space clearance rate and handling time. Moreover, a series of arena sizes may indicate the arena size at which adding space no longer matters, potentially helping to foster a simple way of scaling laboratory results up to natural conditions.

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Author contribution statement SFU and CM conducted the experiments. SFU and JPD analyzed the data and wrote the paper. All authors contributed to editing the paper.

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